Dappled light disrupts prey detection by masking movement

Samuel R. Matchette [a, b]

Innes C. Cuthill [a]

Nicholas E. Scott-Samuel [b]

[a] *School of Biological Sciences, University of Bristol*

[b] *School of Experimental Psychology, University of Bristol*

Corresponding author:

Samuel R. Matchette

+44 (0)117 394 1212

sam.matchette@bristol.ac.uk

School of Biological Sciences

University of Bristol

Bristol Life Sciences Building

24 Tyndall Avenue

Bristol

BS8 1TQ

Authors' copy, accepted by *Animal Behaviour* on 27/05/2019

Prey and ambush predators that rely on concealment face a major constraint: motion breaks camouflage. However, dappled light is a common feature of sunny, vegetated habitats and can, when conditions are windy, become a source of dynamic visual noise. We tested the idea that the latter could mask movement, reducing the risk of detection. Newly-hatched domestic fowl chicks (*Gallus gallus domesticus*), a proxy for wild forest-floor birds, were trained to peck moving, on-screen prey presented amongst two sources of dynamic dappled light: computer-simulated and that created with a mirror ball. Dynamic dapple, however produced, increased the chick's latency to both fixate and peck the prey. Furthermore, we show that dynamic visual noise masks motion in a way that static visual noise does not. This reduction in foraging efficiency should, we predict, have significant consequences for an organism's choice of habitat (as prey), foraging area (as predator) and its pattern of movement within a habitat.

Key words:

Dynamic illumination, dappled light, foraging, motion camouflage, signal masking

Think of the dappled lighting as leaves sway in the wind, or the complex reticulated patterns of light underwater (hereafter 'caustics') created by waves. Dynamic illumination is a common environmental phenomenon, both terrestrially and aquatically, yet investigations of how animals forage, and of visual search more generally, ignore this. Further, the direct influence of dynamic illumination upon behaviour in non-humans is yet to be quantified.

This lack of research is somewhat surprising given that dynamic illumination increases visual complexity by introducing background motion noise. The latter is a known obstacle to signalling, particularly signals that are dynamic (Ord, Peters, Clucas, & Stamps, 2007; Peters, 2013). In such cases, a behavioural adjustment is required to maintain the signal-to-noise ratio (hereafter 'SNR'; Merilaita et al. 2017) and increase the likelihood of that signal being received (Ord et al., 2007; Peters, 2013). Conversely, the opposite is true for camouflage: the prime objective here is to reduce the SNR so that dynamic cues, such as organism movement, go undetected, falling within the distribution of this background motion noise (Fleishman, 1985, 1986). This is an important consideration as motion, in general, is said to 'break' camouflage (Cott, 1940; Hailman, 1977; Hall, Cuthill, Baddeley, Shohet, & Scott-Samuel, 2013; Rushton, Bradshaw, & Warren, 2007; Scott-Samuel, Baddeley, Palmer, & Cuthill, 2011; Stevens, Yule, & Ruxton, 2008; Zylinski, Osorio, & Shohet, 2009).

Data from visual search experiments on humans suggests how dynamic illumination may influence behaviour. Matchette et al. (2018) investigated how prey detection was independently affected by the presence of dappled light and water caustics (both static and dynamic). When asked to capture moving prey items within computer-simulated scenes, human participants were significantly slower and more error-prone when viewing scenes with illumination that was dynamic as opposed to static. We therefore predict that such visual complexity will similarly mask prey movement for foraging animals. However,

74 we cannot assume that other animals, even highly visual predators such as birds,
75 respond to dynamic illumination in the same way as humans for two main reasons. First,
76 the processing of luminance and colour information may differ. For example, birds have
77 a different photoreceptor type, double cones, which seem to drive some or all of their
78 luminance-based visual processing, while humans use pooled signals from medium- and
79 long-wave single cones (Osorio & Vorobyev, 2005). Second, there are differences in the
80 neural structures controlling attentional mechanisms between mammals and other
81 vertebrates (Sridharan, Schwarz, & Knudsen, 2014).

82 We adapted the paradigm of Matchette et al. (2018) for domestic fowl chicks (*Gallus*
83 *gallus domesticus*) as a proxy for wild foraging birds. These birds are easily acquired
84 and trained, and have become common model system for general bird vision, cognition
85 and behaviour (Lisney et al., 2011; Marino, 2017; Miller & Hollander, 2010; Skelhorn &
86 Rowe, 2006; Skelhorn, Rowland, Speed, & Ruxton, 2010). The visual system of domestic
87 fowl is also well characterised (Fantz, 1957a; Ham & Osorio, 2007; Jarvis, Taylor,
88 Prescott, Meeks, & Wathes, 2002; Lisney et al., 2011; Over & Moore, 1981) and they
89 have an omnivorous diet that includes moving invertebrate prey (Marino, 2017). Soon
90 after hatching, chicks will visually follow and peck appropriately at moving objects (Fantz,
91 1957b; Over & Moore, 1981) meaning they are readily trained to a specific foraging task.

92 METHODS

93 *Pre-training and setup*

94 Forty newly-hatched female domestic fowl chicks were obtained from Hy-Line
95 International (www.hyline.com) and housed in the poultry facility of the University of
96 Bristol Veterinary School for the duration of the experiment. By obtaining chicks within
97 24 hours of hatching, these chicks had no prior associations (either good or bad) with
98 the type of lighting and screens used. All procedures were approved by the Animal

Welfare and Ethical Review Body, University of Bristol (UIN/18/047). After the experiments, with veterinary approval, chicks were rehomed to local small-holders.

Upon arrival, each chick was given a unique combination of head, upper back and lower back markings using varying colours of non-toxic paint (Porcimark marking spray, Kruuse, www.kruuse.com) for identification and were housed in the same, 250x50x50 cm, arena with wood chip as substrate. Any initial handling by experimenters was paired with a mealworm (*Tenebrio molitor*): this establishes a positive association with handling and familiarised chicks with the reward food item used in training and experimentation. The latter took place in a separate arena. Water and food were provided ad libitum, via water feeders and trays of chick starter crumb at substrate level (Farmgate, www.forfarmers.co.uk/poultry). The only exception to this was the removal of food trays for a short (30 min) pre-trial food deprivation period to increase the chick's motivation to forage in training and experimental trials.

The experimental arena, located across the room to the housing arena, was a cage measuring 120x50x50 cm with wood chip substrate (Fig. 1a). At one end of this cage was a section (20x50x50 cm) partitioned off using wire mesh. This created an independent 'buddy area': in all training and experimental trials, two chicks were placed in this space to reduce any potential distress for the experimental chicks due to social isolation. A quarter of the chicks (10) were immediately allocated a buddy chick role and played no part as experimental chicks. Throughout training and experimentation, buddy chicks were changed every 25 trials, or sooner if they themselves started to emit distress calls (<5% of trials).

The simulated scenes, stimuli and subsequent experimental task were created and executed in Unreal Engine 4 (Epic Games, www.unrealengine.com) and viewed at 0-20 cm from a gamma-corrected 20″ Philips 200WS monitor (Philips, www.philips.co.uk), with a refresh rate of 75 Hz, an active LCD matrix and a resolution of 1680x1050 pixels.

125 Because the Flicker Fusion Frequency can sometimes exceed 75 Hz (Jarvis et al., 2002;
126 Lisney et al., 2011), the use of a monitor with an active LCD matrix was desirable to
127 ensure that any aversion to the screen (due to a refresh rates less than the FFF) was
128 avoided (Oliveira et al., 2000). This monitor was positioned adjacent to the wire mesh
129 and buried flush to the substrate. Each scene was monochromatic, covered a screen
130 area of 1680x950 pixels with a mean luminance of 80 cd/m^2 and was viewed from a
131 bird's-eye perspective (Fig. 1b). The prey item was a (simulated) three-dimensional
132 sphere with a matt surface and mean luminance equal to that of the background. When
133 viewed from above, as in the experiment, the prey item was a circle of radius 18.7 pixels
134 (Fig. 1c) with apparent three-dimensional shape derived from the realistic projection of
135 light to create shape-from-shading cues (Cook, Qadri, Kieres, & Commons-Miller, 2012).
136 Prey items could appear at any random locus within one of two regions (210x650 pixels)
137 of the scene and, once present, would follow a linear vector towards another random
138 locus in the opposite region (Fig. 1b). Movement was fixed at a speed of 24 mm/s (6.9
139 deg/s) and the prey item continued to move back and forth along this vector for the
140 duration of the trial. This speed was chosen after pilot trials with a prior cohort of chicks,
141 to ensure that moving prey items were detectable, but did not leave the screen too fast
142 to be pecked. Time of appearance, location and subsequent movement vectors were
143 random, picked from discrete uniform distributions using Unreal Engine's random integer
144 generator. Location regions were set such that prey items never left the viewed scene.
145 An Akaso Brave 4 action camera (Akaso, www.akaso.org) was attached to the wire mesh
146 above the monitor to record each trial from above. Recordings (4K resolution, 24 fps and
147 170° viewing angle) were then viewed post-hoc to analyse the chick's behaviour and to
148 measure their responses.

149 Two sources of dappled light were used, one created via a mirror ball and the other via
150 computer simulations (henceforth 'screen dapple'). For the former, a mirror ball

(Showtec, www.showtec.co.uk; 500 mm diameter with 10x10 mm facets, suspended from a light rail) was used in conjunction with a spotlight (Arrilite 800, www.arri.com/lighting) to bathe the entire experimental arena in dappled light. The mirror ball could be left stationary or gently spun to create either static or dynamic dappled light (Fig. 1c). For the screen dapple treatments, Unreal Engine was used to create computer-simulated dappled forest light, identical to that used by Matchette et al. (2018; see Supplementary Material). This dappled light could also be static or dynamic but was localised to the computer screen. There were therefore five treatments in total, in a 2x2+1 design: static mirror-ball dapple, dynamic mirror-ball dapple, static simulated dapple, dynamic simulated dapple, and no dapple illumination (henceforth termed 'absent').

Protocol

Chicks were placed in the start pen and allowed to move towards the monitor to 'forage' for the prey item. If a chick correctly pecked the prey item, a food reward was immediately dropped next to the chick and the trial stopped. A time limit of 2 min was given per trial. This process was repeated five times sequentially for each chick for a given treatment.

Response measures were derived from video recordings. Once a chick had passed a threshold of 10 cm from the screen, at which point it was possible to detect the prey item, a timer was initiated which marked the start of the trial. The time of first fixation of the prey was recorded, as well as the time of the subsequent peck at the prey. 'Fixation' was superficially different to the cursory monocular scans that were common when a chick first entered the arena: the chick adjusts the orientation of its head in the direction of the prey item, allowing full binocular attention, at which point the neck extends and the chick begins to 'stalk' the prey item along its trajectory. Attack Latency (AL) was defined as the overall time from trial start to first correct peck. This comprised Fixation Latency (FL), the time from trial start to first fixation, and Peck Delay, the difference in time between the first fixation and the first correct peck. To check our response measures for experimenter

177 bias, as well as their replicability, an independent referee recorded several response
178 measures from a random sample of videos spanning all treatments which could be
179 compared to the original experimenter recordings.

180 *Training phase and experimental phase*

181 Several training steps were necessary to introduce the task at hand, as well as each
182 component of the experiment (see Appendix). Due to the narrow window for early chick
183 learning, only chicks that attained 80% success rate (to peck the prey item and consume
184 the reward) in a given training block would progress. Any chicks that failed to reach this
185 criterion within the allocated blocks were converted to 'buddy' chicks. Of the remaining
186 thirty chicks, eighteen met the criterion and entered the experiment.

187 The experimental phase mimicked the format of the training phase, but with a more
188 complex and context-relevant background. This comprised a single image of leaf litter,
189 sourced from the software's default asset package, which was tiled repeatedly to make
190 up a background scene (Fig. 1d). We used the selected background "out of the box",
191 with RGB range and mean values as supplied by Unreal Engine, as these were already
192 judged to be realistic and, in any case, precise simulation of a real forest-floor
193 background (that these chicks had never experienced) was unimportant for the
194 experiment's goals. The target luminance was then adjusted to match the mean
195 background luminance. All treatments were run twice and in a randomised order, totalling
196 10 trials (2 x 5) per chick for each treatment. If a chick did not peck the target within 1
197 min, the trial was ended and the chick was returned to the home arena.

198 All statistical analyses were performed in R 3.3.2 (R Foundation for Statistical
199 Computing, www.R-project.org) and utilised generalized linear mixed models (function
200 glmer in the lme4 package; Bates et al., 2017). The response variables were Attack
201 Latency, Fixation Latency and Peck Delay, all with Gamma error and inverse link
202 functions. The gamma link was used because of positive skew in the raw time data. The

full model included the fixed effect treatment and the random effect of chick ID. The change in deviance between models with and without the predictors of interest was tested against a χ^2 distribution with degrees of freedom equal to the difference in degrees of freedom between the models. Treatment effects were examined using a custom contrast matrix that represented the a priori comparisons of interest: the main effects of Display (mirror-ball vs screen dapple), Motion (static vs dynamic) and their interaction), plus a set of pairwise comparisons between each treatment and the dapple-absent control. This matrix has more contrasts than we have degrees of freedom, so we corrected for multiple testing using the single step method provided by the multcomp package (Hothorn, Bretz, & Westfall, 2008). The test statistic for these contrasts was the standardised normal deviate (*z*). For those interested in other comparisons, the full set of pair-wise comparisons, using the Tukey procedure in multcomp, is also provided.

To check our response measures for experimenter bias, as well as their replicability, nine, naive, independent volunteers estimated both fixation latency and pecking delay from 25 sample videos spanning all treatments. The 10 sets of timings for each of the response measures were then compared using the intra-class correlation coefficient (Shrout & Fleiss, 1979); function ICC from the R package psych (Revelle, 2017). Because bias is of interest as well as correlation, we also compared these nine volunteers' data to those of the original experimenter using paired t-tests (see Appendix).

Ethical note

Forty newly-hatched female domestic fowl chicks were obtained from Hy-Line International (www.hyline.com) and housed in the poultry facility of the University of Bristol Veterinary School for the duration of the experiment. All procedures were approved by the Animal Welfare and Ethical Review Body, University of Bristol (UIN/18/047).

228 Upon arrival, each chick was given a unique combination of head, upper back and lower
229 back markings using varying colours of non-toxic paint (Kruuse, www.kruuse.com) for
230 identification and were housed in the same, 250x50x50 cm, arena with wood chip as
231 substrate. Any initial handling by experimenters was paired with a mealworm (*Tenebrio*
232 *molitor*): this establishes a positive association with handling and familiarised chicks with
233 the reward food item used in training and experimentation. The latter took place in a
234 separate arena. Water and food were provided ad libitum, via water feeders and trays of
235 chick starter crumb at substrate level (Farmgate, www.forfarmers.co.uk/poultry). The
236 only exception to this was the removal of food trays for a short (30 min) pre-trial food
237 deprivation period to increase the chick's motivation to forage in training and
238 experimental trials.

239 The housing arena was subject to a light cycle that matched the ambient day-light cycle,
240 achieved using ceiling daylight mimicking lamps (GEWISS, www.gewiss.com; twin 26 W
241 LED) running in high-frequency (30 kHz+) ballasts, well above the c.60 Hz CFF (critical
242 flicker fusion frequency) of domestic fowl (e.g. 13,14). The ambient temperature was
243 maintained at 25-28 °C using multiple 175 W infrared heat lamps (General Electric,
244 www.gelighting.com) positioned on a light rail c.60 cm above the arena.

245 The housing arena also contained multiple objects that the chicks would encounter in
246 the experimental arena, including a low perch, a hanging mirror ball (50 cm in diameter)
247 and a computer monitor. This exposure minimised any neophobic responses to these
248 items when placed in the experimental arena. For example, the computer monitor was
249 buried into the substrate such that chicks could walk over the screen in an identical
250 manner to the experimental arena. Videos of training background scenes (see below)
251 could then be presented on a continuous loop for the duration of the daylight hours.

252 The experimental arena, located across the room to the housing arena, was a cage
253 measuring 120x50x50 cm with wood chip substrate (Fig. 1a). At one end of this cage

was a section (20x50x50 cm) partitioned off using wire mesh. This created an independent 'buddy area': in all training and experimental trials, two chicks were placed in this space to minimise distress for the experimental chicks due to social isolation.

Throughout the duration of this experiment, there were no: potentially harmful manipulations, invasive samples, trapping, tags, radio-transmitters, data loggers or transponders. No procedures could potentially lead to distress and pain.

Once the experimental phase was complete, all chicks were donated to free-range small-holdings.

RESULTS

When domestic fowl were presented with moving prey items, the Attack Latency was significantly longer when in the presence of dynamic computer-simulated dappled light than dynamic mirror ball dapple light, and both of these treatments had longer latencies than any other treatments (treatment $\chi^2_4 = 269.87$, $P < 0.001$; Fig. 2 & Table 1: Attack Latency). Breaking down this overall treatment effect, there was a significant interaction between Display and Motion ($z = 3.95$, $P < 0.001$) so, to establish why, mirror-ball and screen dapple treatments were analysed separately. Dynamic dapple increasing attack latency in both conditions, but more than twice as much with screen dapple (104% increase; $\chi^2_1 = 178.77$, $P < 0.001$) than with mirror-ball dapple (41% increase; $\chi^2_1 = 56.07$, $P < 0.001$). Attack latency for both dynamic dapple treatments was significantly longer than in the dapple-absent control (mirror: $z = 5.31$, $P = 0.111$; screen: : $z = 9.64$, $P = 0.111$). The Attack Latency under static mirror-ball dapple did not differ from that in the absence of dappled light ($z = 2.30$, $P = 0.111$), but latency in the absence of dappled light was longer than in the static screen-dapple treatment $z = 4.30$, $P < 0.001$).

The above treatment differences were largely driven by Fixation Latency, with the pattern and significance of treatment differences matching those for Attack Latency (treatment

280 χ^2_4 = 601.87, P < 0.001; Fig. 2 & Table 1: Fixation Latency). There was a significant
281 interaction between Display and Motion (z = 7.09, P < 0.001). Analysing mirror-ball and
282 screen dapple treatments separately, dynamic dapple increased Fixation Latency in both
283 conditions, but far more with screen dapple (164% increase; χ^2_1 = 247.70, P < 0.001)
284 than with mirror-ball dapple (19% increase; χ^2_1 = 15.35, P < 0.001). Attack latency for
285 both dynamic dapple treatments was significantly longer than in the dapple-absent
286 control (mirror: z = 3.06, P = 0.013; screen: : z = 16.43, P < 0.001). The Attack Latencies
287 under static mirror-ball dapple and screen dapple did not differ from that in the absence
288 of dappled light (z = 0.48, P = 0.984, z = -0.55, P = 0.975, respectively).
289 The treatment differences in the delay from fixation to pecking were significant but
290 simpler (χ^2_4 = 108.58, P < 0.001; Fig. 2 & Table 1: Peck Delay). There was no significant
291 interaction between Display and Motion (z = 0.184, P = 1.000) but main significant main
292 effects of Screen and Motion. Dynamic dapple increased peck delay by 53% compared
293 to static (z = -7.47, P < 0.001) and mirror dapple increased delay by 86% compared to
294 screen-based dapple (z = -5.26, P < 0.001). Compared to the dapple-absent control,
295 dynamic mirror dapple increased peck delay (z = -4.45, P < 0.001), static screen dapple
296 reduced it (z = 5.50, P < 0.001), and both static mirror (z = 2.39, P = 0.093) and dynamic
297 screen dapple (z = 0.78, P = 0.916) showed no significant difference.
298 DISCUSSION
299 The ability of domestic fowl to forage for on-screen prey is influenced by the presence of
300 dynamic dappled light in the same manner as in humans (Matchette et al., 2018).
301 Moreover, this effect is consistent irrespective of the method used to create the dynamic
302 dappled light: both screen dapple and mirror ball dapple increased the latency to fixate
303 and to attack relative to their static counterparts.
304 These data could be explained in several ways. They could be a consequence of (i) a
305 neophobic response to the dynamic dappled light. Neophobia is a common response of

306 domestic fowl and, therefore, efforts were made to ensure this was minimised: chicks
307 were familiarised with each independent experimental feature during training and only
308 chicks that reached a consistent response threshold were taken on to the experimental
309 phase. The data could be also explained in terms of (ii) a non-specific visual distraction
310 from the task at hand induced by the dappled light. This seems unlikely given that the
311 latency to fixate was higher for screen dapple treatments than for mirror dapple (median
312 of 2.3 > 1.1 s), suggesting that the interference of visual field was localised to the search
313 area rather than a non-specific distraction. Another possible reason for the results seen
314 is that (iii) the regions of dappled light represent a more visually complex environment
315 and therefore reduce search efficiency, an effect already highlighted in birds and humans
316 (Dimitrova & Merilaita, 2010; Merilaita et al., 2017; Xiao & Cuthill, 2016). However, this
317 is unlikely given that there is no effect of static dapple treatments upon successful
318 foraging, which represent equally spatially-complex environments. The most convincing
319 explanation is that (iv) dappled light lowers the SNR: the specific features of the prey that
320 are used for detection and the subsequent attack are drowned out by the moving dappled
321 light (Merilaita et al., 2017). Both sources of dappled light create motion, luminance and
322 edge noise, all features used to discriminate a target from the background. The greater
323 effect of screen dapple versus mirror ball dapple is consistent with this, because the
324 former creates more profound moving false luminance edges in the specific area the
325 target is to be found.

326 In contrast, static dapple, whether produced by mirror ball or only on the computer
327 screen, has little, if any, effect. This might seem surprising because a scene with dappled
328 light has a higher contrast range than without and therefore would appear more visually
329 complex (Dimitrova & Merilaita, 2010; Dimitrova, Stobbe, Schaefer, & Merilaita, 2009;
330 Xiao & Cuthill, 2016). Further, these multiple high contrast light points, particularly for
331 static mirror ball dapple, might act as distractors (Dimitrova et al., 2009). Nevertheless,

the chicks did not appear to be affected: indeed, the peck delay was slightly but significantly longer for scenes with an absence of dappled light than static screen dappled light. A key take-home message is therefore that static noise does not mask dynamic signals (the moving target), but dynamic noise does.

An important methodological note is that, although two sources of dappled light were used that differed in their 'scope of influence' (global or limited to screen), they also differed in terms of spatial structure and the dynamic of dappling. Of the two, screen dapple is a more realistic recreation as it is modelled to match the spatiotemporal properties of real forest dapple flicker. In contrast, mirror ball dapple represented a more predictable light flicker, a product of the uniform mirror ball facets: light spots that move along a parallel trajectory at roughly a constant speed and spacing. In addition, due to its top-down projection, mirror ball dapple could be momentarily occluded by the chick itself and may not consistently project upon an area that the chick is investigating, possibly resulting in a ceiling effect. Indeed, this may be the reason for the differences in fixation latency between the two dynamic treatments and why there was minimal effect of static mirror ball dapple versus the absent control. Nevertheless, mirror ball dapple provides an alternative form of dapple that, when dynamic, still exerts an influence over the ability of chicks to forage successfully.

The presence of dynamic illumination within a habitat has been closely associated with aspects of concealment, colouration and perception. For example, the vertical barring and vermiculation of fish patterns have been linked to the influence of water caustics (McFarland & Loew, 1983), while some felid coats may have been similarly influenced by the presence of dappled light within a habitat (Allen, Baddeley, Cuthill, & Scott-Samuel, 2012). The intensity of water caustic flicker could also have played a significant role in the initial evolution of colour vision (Maximov, 2000). Moreover, the inconsistencies of signal (e.g. in time, space, angle of view and perceived hue), caused

by moving through inconsistent illumination, is likely to impact feature binding of individuals (Espinosa & Cuthill, 2014; Murali, 2018) and the perception of group movement (Murali, Kumari, & Kodandaramaiah, 2019).

Thus, one may expect dynamic illumination, such as dappled light, to have a wider remit of influence, extending to visually-mediated behaviours: where organisms choose to live (as prey), forage (as predators) and display (sexual signals), as well as the pattern of movement used by an organism within a habitat. For example, for mobile prey organism during periods of dynamic dappled light, when the relative safety of movement outweighs that when dappled light is static, one may expect an increase in foraging and commutes between shelters, in conjunction with a lesser need for group or protean movement. A shift towards non-foraging behaviours or foraging techniques associated with non-visual senses may also be expected in predators under the same conditions.

ACKNOWLEDGEMENTS

We thank the animal management team at the University of Bristol Veterinary School for the use of their facilities and for sustaining the chicks throughout the study. Thanks also to Karin Kjernsmo (for her support and knowledge) and indirectly to Jolyon Troscianko (for helpful information with chick training), as well as our nine volunteers for repeatability analysis. Thank you to Sami Merilaita and an anonymous referee for helpful suggestions on a previous version of the manuscript.

FUNDING

This work was supported by SM's CASE Studentship from the Engineering and Physical Sciences Research Council, UK, and QinetiQ plc, and EPSRC grant EP/M006905/1 to NSS, ICC and R. Baddeley.

REFERENCES

Allen, W. L., Baddeley, R. J., Cuthill, I. C., & Scott-Samuel, N. E. (2012). A quantitative

383 test of the predicted relationship between countershading and lighting
384 environment. *American Naturalist*, *180*(6), 762–776.
385 https://doi.org/10.1086/668011

386 Bates, D., Maechler, M., Bolker, B., Walker, S., Haubo, R., Christensen, B., Singmann
387 H., Dai B., Grothendieck G., Green P. (2017). lme4: Linear Mixed-Effects Models
388 using “Eigen” and S4. Comprehensive R Archive Network (CRAN). Retrieved from
389 https://cran.r-project.org/web/packages/lme4/index.html

390 Cook, R. G., Qadri, M. A. J., Kieres, A., & Commons-Miller, N. (2012). Shape from
391 shading in pigeons. *Cognition*, *124*, 284–303.

392 Cott, H. B. (1940). *Adaptive Colouration in Animals*. London, UK: Methuen & Co. Ltd.

393 Dimitrova, M., & Merilaita, S. (2010). Prey concealment: visual background complexity
394 and prey contrast distribution. *Behavioral Ecology*, *21*(1), 176–181.
395 https://doi.org/10.1093/beheco/arp174

396 Dimitrova, M., Stobbe, N., Schaefer, H. M., & Merilaita, S. (2009). Concealed by
397 conspicuousness: distractive prey markings and backgrounds. *Proceedings of the*
398 *Royal Society B: Biological Sciences*, *276*(1663), 1905–1910.
399 https://doi.org/10.1098/rspb.2009.0052

400 Espinosa, I., & Cuthill, I. C. (2014). Disruptive colouration and perceptual grouping.
401 *PLoS ONE*, *9*(1), e87153. https://doi.org/10.1371/journal.pone.0087153

402 Fantz, R. L. (1957a). Form preferences in newly hatched chicks. *Journal of*
403 *Comparative and Physiological Psychology*, *50*(5), 422–430.
404 https://doi.org/10.1037/h0044973

405 Fantz, R. L. (1957b). Form preferences in newly hatched chicks. *Journal of*
406 *Comparative and Physiological Psychology*, *50*(5), 422–430.

https://doi.org/10.1037/h0044973

Fleishman, L. J. (1985). Cryptic movement in the vine snake *Oxybelis aeneus*. *Copeia*, *1985*(1), 242–245. https://doi.org/10.2307/1444822

Fleishman, L. J. (1986). Motion detection in the presence and absence of background motion in an *Anolis* lizard. *Journal of Comparative Physiology A*, *159*(5), 711–720. https://doi.org/10.1007/BF00612043

Hailman, J. P. (1977). *Optical Signals: Animal Communication and Light*. Bloomington, IN, USA: Indiana University Press.

Hall, J. R., Cuthill, I. C., Baddeley, R. J., Shohet, A. J., & Scott-Samuel, N. E. (2013). Camouflage, detection and identification of moving targets. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1758), 20130064. https://doi.org/10.1098/rspb.2013.0064

Ham, A. D., & Osorio, D. (2007). Colour preferences and colour vision in poultry chicks. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1621), 1941–1948. https://doi.org/10.1098/rspb.2007.0538

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*(3), 346–363.

Jarvis, J. R., Taylor, N. R., Prescott, N. B., Meeks, I., & Wathes, C. M. (2002). Measuring and modelling the photopic flicker sensitivity of the chicken (*Gallus g domesticus*). *Vision Research*, *42*, 99–106.

Lisney, T. J., Rubene, D., Rózsa, J., Løvlie, H., Håstad, O., & Ödeen, A. (2011). Behavioural assessment of flicker fusion frequency in chicken *Gallus gallus domesticus*. *Vision Research*, *51*(12), 1324–1332. https://doi.org/10.1016/J.VISRES.2011.04.009

Marino, L. (2017). Thinking chickens: a review of cognition, emotion, and behavior in the domestic chicken. *Animal Cognition*, *20*(2), 127–147. https://doi.org/10.1007/s10071-016-1064-4

Matchette, S. R., Cuthill, I. C., & Scott-Samuel, N. E. (2018). Concealment in a dynamic world: dappled light and caustics mask movement. *Animal Behaviour*, *143*, 51–57. https://doi.org/10.1016/j.anbehav.2018.07.003

Maximov, V. V. (2000). Environmental factors which may have led to the appearance of colour vision. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *355*(1401), 1239–1242. https://doi.org/10.1098/rstb.2000.0675

McFarland, W. N., & Loew, E. R. (1983). Wave produced changes in underwater light and their relations to vision. *Environmental Biology of Fishes*, *8*(3–4), 173–184. https://doi.org/10.1007/BF00001083

Merilaita, S., Scott-Samuel, N. E., & Cuthill, I. C. (2017). How camouflage works. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1724), 20160341. https://doi.org/10.1098/rstb.2016.0341

Miller, C. W., & Hollander, S. D. (2010). Predation on heliconia bugs, *Leptoscelis tricolor*: examining the influences of crypsis and predator color preferences. *Canadian Journal of Zoology*, *88*(1), 122–128. https://doi.org/10.1139/Z09-128

Murali, G. (2018). Now you see me, now you don't: dynamic flash coloration as an antipredator strategy in motion. *Animal Behaviour*, *142*, 207–220. https://doi.org/10.1016/j.anbehav.2018.06.017

Murali, G., Kumari, K., & Kodandaramaiah, U. (2019). Dynamic colour change and the confusion effect against predation. *Scientific Reports*, *9*(1), 274. https://doi.org/10.1038/s41598-018-36541-7

455 Oliveira, R. F., Rosenthal, G. G., Schlupp, I., McGregor, P. K., Cuthill, I. C., Endler, J.
456 A., … Waas, J. R. (2000). Considerations on the use of video playbacks as visual
457 stimuli: The Lisbon workshop consensus. *Acta Ethologica*, *3*, 61–65.

458 Ord, T. J., Peters, R. A., Clucas, B., & Stamps, J. A. (2007). Lizards speed up visual
459 displays in noisy motion habitats. *Proceedings of the Royal Society B: Biological*
460 *Sciences*, *274*(1613), 1057–1062. https://doi.org/10.1098/rspb.2006.0263

461 Osorio, D., & Vorobyev, M. (2005). Photoreceptor spectral sensitivities in terrestrial
462 animals: adaptations for luminance and colour vision. *Proceedings of the Royal*
463 *Society B: Biological Sciences*, *272*, 1745–1752.

464 Over, R., & Moore, D. (1981). Spatial acuity of the chicken. *Brain Research*, *211*(2),
465 424–426. https://doi.org/10.1016/0006-8993(81)90967-7

466 Peters, R. A. (2013). Noise in visual communication: motion from wind-blown plants. In
467 H. Brumm (Ed.), *Animal Communication and Noise* (Vol. 2, pp. 311–330).
468 Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-41494-7_11

469 Prescott, N. B., Wathes, C. M., & Jarvis, J. R. (2003). Light, vision and the welfare of
470 poultry. *Animal Welfare*, *12*, 269–288.

471 Revelle, W. R. (2017). psych: Procedures for Personality and Psychological Research.
472 Evanston, Illinois, USA: Northwestern University. Retrieved from
473 https://www.scholars.northwestern.edu/en/publications/psych-procedures-for-
474 personality-and-psychological-research

475 Rushton, S. K., Bradshaw, M. F., & Warren, P. A. (2007). The pop out of scene-relative
476 object movement against retinal motion due to self-movement. *Cognition*, *105*(1),
477 237–245. https://doi.org/10.1016/j.cognition.2006.09.004

478 Scott-Samuel, N. E., Baddeley, R. J., Palmer, C. E., & Cuthill, I. C. (2011). Dazzle

camouflage affects speed perception. *PLoS ONE*, *6*(6). https://doi.org/10.1371/journal.pone.0020233

Shrout, P. E., & Fleiss, J. L. (1979). Intraclass correlations: uses in assessing rater reliability. *Psychological Bulletin*, *86*, 420–428.

Skelhorn, J., & Rowe, C. (2006). Taste-rejection by predators and the evolution of unpalatability in prey. *Behavioral Ecology and Sociobiology*, *60*(4), 550–555. https://doi.org/10.1007/s00265-006-0199-8

Skelhorn, J., Rowland, H. M., Speed, M. P., & Ruxton, G. D. (2010). Masquerade: camouflage without crypsis. *Science*, *327*(5961), 51. https://doi.org/10.1126/science.1181931

Sridharan, D., Schwarz, J. S., & Knudsen, E. I. (2014). Selective attention in birds. *Current Biology*, *24*(11), R510.

Stevens, M., Yule, D. H., & Ruxton, G. D. (2008). Dazzle coloration and prey movement. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1651), 2639–2643. https://doi.org/10.1098/rspb.2008.0877

Xiao, F., & Cuthill, I. C. (2016). Background complexity and the detectability of camouflaged targets by birds and humans. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1838), 20161527. https://doi.org/10.1098/rspb.2016.1527

Zylinski, S., Osorio, D., & Shohet, A. J. (2009). Cuttlefish camouflage: context-dependent body pattern use during motion. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1675), 3963–3969. https://doi.org/10.1098/rspb.2009.1083

503

504

505

506

507

508

509

510

511

512

513

514

515 Tables

516

517

518

Table 1. Pair-wise treatment comparisons for overall Attack Latency and its components (Fixation Latency and Peck Delay).

	Attack Latency					Fixation Latency					Peck Delay				
	Abs	MS	MD	SS	SD	Abs	MS	MD	SS	SD	Abs	MS	MD	SS	SD
Abs	—	0.136	<0.001	<0.001	<0.001	—	0.988	0.018	0.981	<0.001	—	0.111	<0.001	<0.001	0.932
MS	2.30	—	<0.001	0.280	<0.001	0.48	—	0.004	0.831	<0.001	2.39	—	<0.001	0.012	0.485
MD	-5.31	-7.30	—	<0.001	<0.001	-3.06	-3.50	—	0.071	<0.001	-4.45	-6.24	—	<0.001	<0.001
SS	4.30	1.95	9.27	—	<0.001	-0.54	-1.03	2.57	—	<0.001	5.50	3.18	8.84	—	<0.001
SD	-9.64	-11.14	-4.97	-13.03	—	-16.44	-16.50	-14.56	-16.64	—	0.78	-1.60	4.91	-4.72	—

Lower-left-hand triangle of each matrix are Tukey-type t-tests; upper-right-hand triangles are corresponding p-values. Abbreviations for dapple treatments are Abs: absent; MS: mirror static; MD: mirror dynamic; screen static; SD: screen dynamic.

519

520

Table.A1 The number of trials completed by each chick during both the training and experimental phases of the study.

Training phase:	Screen	Prey item	Dappled light	Number of trials per chick
Step 1	White	Stationary	Absent	25
Step 2	White	Moving	Absent	15
Step 3:				
a	White	Moving	Mirror ball: static	5
b	White	Moving	Mirror ball: dynamic	10
Step 4:				
a	White	Moving	Simulated: static	5
b	White	Moving	Simulated: dynamic	10
Experimental phase:				
Treatment 1	Leaf litter	Moving	Absent	10
Treatment 2	Leaf litter	Moving	Mirror ball: static	10
Treatment 3	Leaf litter	Moving	Mirror ball: dynamic	10
Treatment 4	Leaf litter	Moving	Simulated: static	10
Treatment 5	Leaf litter	Moving	Simulated: dynamic	10

521

522

523

524

525

526

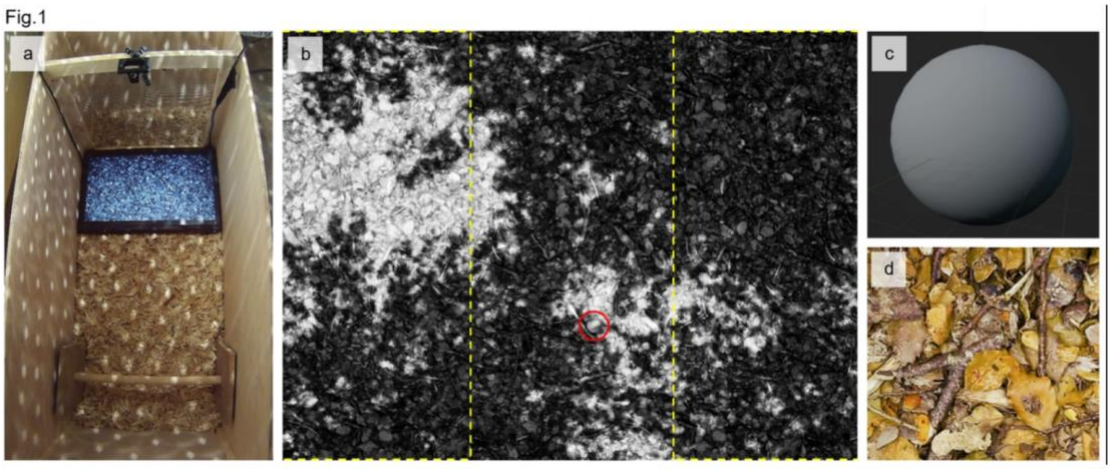
527

528

529

530 Figures

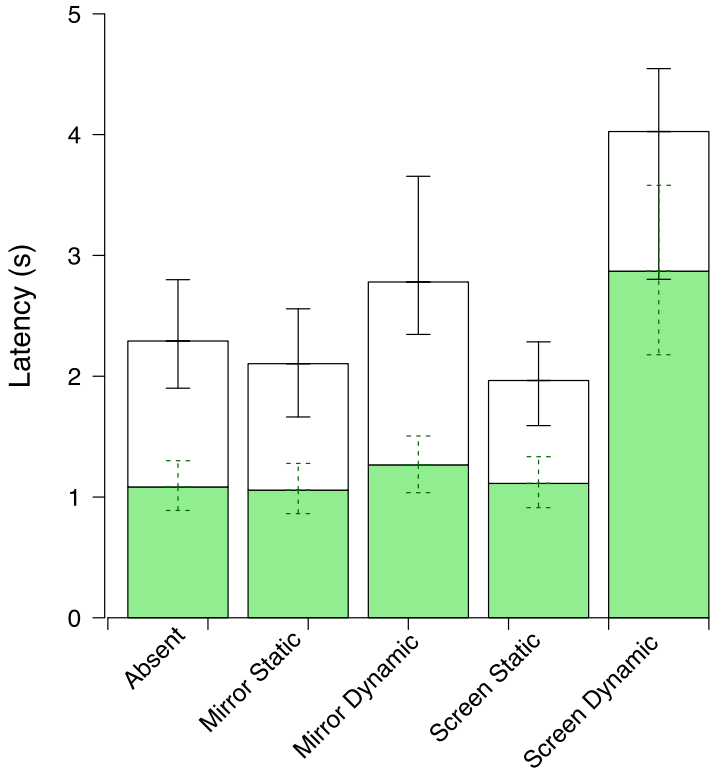
Fig.1



531

532 Figure 1 (a) A photograph of the experimental arena in the presence of mirror ball
533 dappled light. Chicks were lowered in at the start pen (denoted by the horizontal perch)
534 and moved towards the stimuli monitor to forage. The buddy arena (beyond the monitor)
535 was physically, but not visually, divided from the experimental arena with wire mesh. The
536 recording device position can be seen on top of the wire mesh divider. (b) Screenshot of
537 experimental trial. The two regions denoted by the dashed yellow lines are the possible
538 prey item appearance areas (no lines were present in the actual trials). The prey item
539 (artificially highlighted by a red circle) is mid-way through moving from one appearance
540 area towards the other. (c) A close-up of the prey item outside of the experimental
541 context. (d) Screenshot of the tiled leaflitter image used as experimental backdrop. This
542 image was converted to monochrome for the purpose of the experiment. (b – d) These
543 figures are reproduced with permission from Matchette et al. (2018).

544



545

546 Figure 2 - Mean fixation latency (green) and overall attack latency (white) of chicks
547 across the five treatments. The difference between the two latencies represents Peck
548 Delay. Error bars for Fixation Latency (dark green) and Attack Latency (black) indicate
549 95% confidence intervals derived from bootstrapping the linear mixed models (1000
550 simulations, function confint.merMod(method='boot) from the R package lme4)..

551

552 Appendix

553 Part of this text are reproduced with permission from Matchette et al. (2018).

554 *Set-up: housing arena*

555 The housing arena was subject to a light cycle that matched the ambient day-light cycle,
556 achieved using ceiling daylight mimicking lamps (GEWISS, www.gewiss.com; twin 26 W
557 LED) running in high-frequency (30 kHz+) ballasts, well above the c.60 Hz CFF (critical
558 flicker fusion frequency) of domestic fowl (e.g. 13,14). The ambient temperature was
559 maintained at 25-28 °C using multiple 175 W infrared heat lamps (General Electric,
560 www.gelighting.com) positioned on a light rail c.60 cm above the arena.

561 In addition to food and water, the housing arena also contained multiple objects that the
562 chicks would encounter in the experimental arena, including a low perch, a hanging
563 mirror ball (50 cm in diameter) and a computer monitor. This exposure minimised any
564 neophobic responses to these items when placed in the experimental arena. For
565 example, the computer monitor was buried into the substrate such that chicks could walk
566 over the screen in an identical manner to the experimental arena. Videos of training
567 background scenes (see below) could then be presented on a continuous loop for the
568 duration of the daylight hours.

569 *Set-up: experimental arena*

570 At the opposite end to the monitor and buddy arena was a horizontal wooden perch used
571 to loosely segregate a 'start pen' from which chicks could begin each trial. To ensure an
572 ambient temperature of 25-28 °C, as in the housing arena, a 175 W infrared heat lamp
573 was also present.

574 *Training phase*

575 The training phase involved four steps with stimuli displayed upon the monitor, with the
576 screen set to white (Table A1). Each step was conducted within the experimental arena

and aimed to introduce key elements of the later experiment. The first step introduced the computer-generated, spherical prey item. This step was critical to establish an association between the prey on the screen and reward. To achieve this, prey items remained stationary with a mealworm placed beside (so as not to obscure the target). The second step introduced a moving prey item; a food reward was initially given once the chick had approached the prey item, which encouraged later pecking. The third and fourth steps then introduced a moving prey item in the presence of dappled light created via the mirror ball and computer simulations respectively. Both forms of dappled light were initially introduced statically, then later dynamically. Each chick completed no more than three training blocks in a day, with at least a 1.5 -hour gap between each block.

Experimental phase

The experimental phase repeated the format of training steps 2-4, but with a more complex background. Throughout the experimental phase, chicks pecked the target within 1 min in 82% of trials (mean Attack Latency 3.2 s, median 2.1 s, range 0.6 - 45.3 s) and all chicks did so in at least five of the 10 trials per treatment. Failures to peck were associated with particular chicks rather than particular treatments (only two chicks completed as few as five trials for a treatment and these two chicks completed < 10 trials for all, and four of the five, treatments respectively).

Screen dapple generation

The simulated scene was created and executed in Unreal Engine 4 (Epic Games, www.unrealengine.com). There were seven key components that formed the core of each experimental zone: (from bottom up) floor, spawn areas, prey item, camera item, tree static mesh collection and the lighting systems. Each had particular settings and 'blueprints' associated, which could be coded in various ways to alter performance and behaviour. Multiple experimental zones were used.

The floor component was a standard plane static mesh coated in a default material acquired from the free demonstration asset package, 'Kite Demo'. The material attached to the floor component ('forest_path_001A') was a tiled, high quality image of leaf litter (Fig. 1). This formed the backdrop to all dappled light trials in this experiment. Set just upon this were two transparent box meshes that would act as 'spawn' (appearance) areas. For any given trial, a prey item would appear at a random location within one appearance area (the 'origin' point), while another random location would be selected from the opposite appearance area (the 'destination' point) to create a random movement vector for the prey item. The prey item was then set to move (at any desired speed) along the random vector. Upon arrival, the prey item would reverse the movement (at the same speed) back towards the origin point. Once here, the process would repeat until the end of the trial.

Above this ground activity, a camera item was positioned, which would provide the player view for each trial. The camera item was rotated 90 degrees to the floor component and had equalised RGB values, creating a monochrome birds-eye view of the leaf litter backdrop. Between this component and the lighting systems were a collection of randomly-positioned, pre-made model tree static meshes, also of the 'Kite Demo' assets package. When paired with the lighting systems above, these cast the characteristic dappled light shadows across the floor component. Each experimental zone had a unique arrangement of trees and therefore a unique arrangement of shadows. Crucially, a highly-editable noise component could be added to create a range of dappled light flickers and dynamic shadows, to mimic the changing strength of wind. High above each zone was a directional light source and a skylight. Each had an intensity scale which would alter both the light intensity (brightness) and the shadow intensity (darkness).

Repeatability and bias

For fixation latency, the intra-class correlation coefficient was 0.82 (95% c.i. 0.73 - 0.90; $F_{24,216} = 47.0$, $P < 0.001$). In pair-wise tests, there was no difference between the original experimenter's data and those of the nine naive volunteers (range of mean differences: -0.05 to 0.04 s, five means being negative and 4 positive; $0.12 < t_{24} < 0.99$; $0.334 < P < 0.907$). For pecking delay, the intra-class correlation coefficient was 0.98 (95% c.i. 0.96 - 0.99; $F_{24,216} = 462.0$, $P < 0.001$). In pair-wise tests, there was no difference between the original experimenter's data and those of eight of the nine naive volunteers (range of mean differences: -0.04 to 0.05 s, five means being negative and 4 positive; $0.05 < t_{24} < 1.84$; $0.079 < P < 0.962$). One rater's pecking delay times were significantly longer than the original experimenter's (mean difference: 0.25 s; $t_{24} = 4.19$, $P < 0.001$), but this rater's times were also significantly longer than those of the eight other naive raters (range of mean differences: 3.13 to 0.30 s; $3.13 < t_{24} < 4.79$; all $P < 0.005$). Therefore, this rater was the outlier and the original experimenter's data were unbiased compared to those of the others. the original experimenter's data were therefore considered suitable estimates for further analysis.